

# The Pupal Forewing Tracheation of Lepidoptera

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## Introduction

It is well known that the wing venation is led from the tracheation. Then, the examination of pupal tracheation is important to determine the homology of wing venation but our knowledge of the pupal tracheation pattern is still incomplete for this purpose. In Lepidoptera, several patterns of pupal tracheation were reported for restricted groups, but the systematic analysis of the patterns has not been carried out in the entire scope of the order. In this paper the author searched the tracheation of the pupal forewings of almost all families of Japanese Lepidoptera, and determined and classified the types of tracheal patterns. Moreover, the tendency of the pattern differentiation was presumed and relationship between the vein and the trachea was discussed.

## Material and Methods

The living pupae of Japanese Lepidoptera represent 44 families were examined. These pupae were bred from the larvae which took in the field.

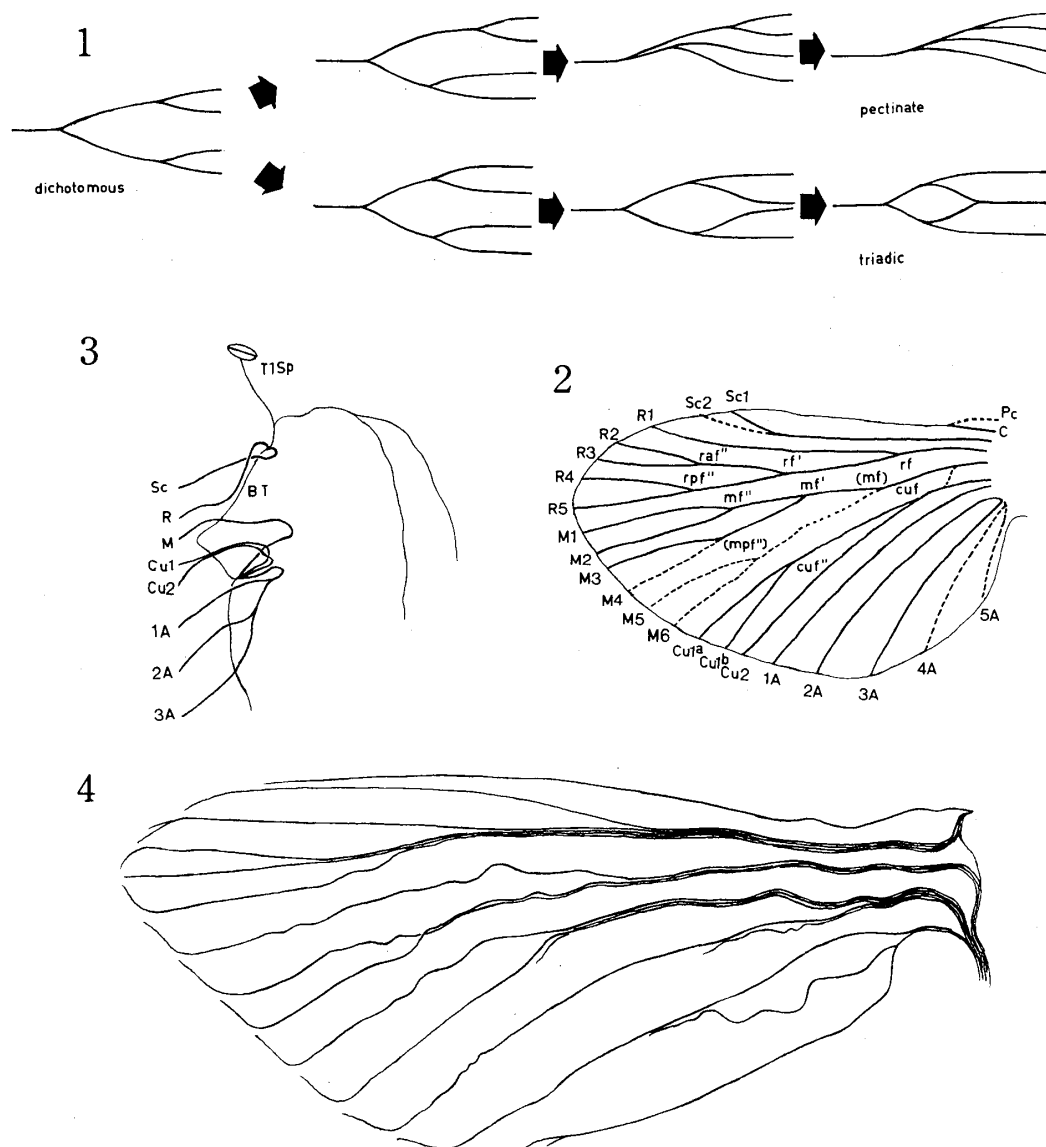
As a rule, the pupal wing tracheation of Lepidoptera can be easily observed at just pupation under a binocular microscope. When the observation is difficult, the living pupa is placed in a freezer and is frozen up rapidly. It is thawed out after about ten hours and is lightly rubbed on the wing cuticular. As the costal area of the forewing is occasionally covered with antenna in some species of Zygaenidae (Fig. 8B), Geometridae (Fig. 14K), Saturniidae (Fig. 16C) and so on, the frozen pupal forewing is removed along its dehiscence by a knife and is separated from the hindwing. The tracheation pattern is visible through the wing membrane.

## The Pupal Wing Tracheation of Lepidoptera

The three branching types, dichotomous, pectinate and triadic, of the wing veins or tracheae have been known but the last two may be readily derived from the first one. The dichotomous-type branching is suitable hydrodynamically for an even distribution of blood, whereas the triadic-type branching seems to be rather difficulty so. The general pattern of the pupal wing tracheation known in the past is that

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many (fifteen in general) tracheae derive from five stems\*, subcosta (Sc), radius (R), media (M), cubitus (Cu) and anal (A), starting from the axilla and some tracheae partly coalesce with adjoining ones. However, the tracheae seem to run from the axilla in



Figs. 1-4. Fig. 1. Three branching types in the tracheation and their supposed transforming process. Fig. 2. The archetype wing venation (modified from SNODGRASS, 1935). All the signs indicating the branching points are those used in this paper. Fig. 3. The basal portion of the tracheal bundles in the forewing of *Hyboma adauca* WARREN (Noctuidae). T1Sp: Prothoracic spiracle; BT: basal trachea connecting with spiracle and wing tracheae. Fig. 4. The pupal forewing tracheation showing the bundles, which are constructed by pleural tracheae, in *Latoia lepida* CRAMER (Limacodidae).

\* NOHIRA (1947) observed that these stems were adjoined at the tripartite points of Sc, R and M + Cu + A with the basal trachea being led from the spiracle. But, the author supports MAKIBAYASHI and HIROHATA's (1980) suggestion that the adjoining occurs at the bipartite points of Sc + R and M + Cu + A (Fig. 3). It is known on the circulation of blood in the wing that blood flows through C, R and M tracheae and returns through Cu and A tracheae. The view may need an amendment that blood flows through Sc and R tracheae and returns through M, Cu and A tracheae.

a bundle for each five stem and deflect from the bundle at fixed points in original. And two deflecting tracheae are often so close to each other that they appear to coalesce into one or one of them vanishes. This hypothesis comes from the observation of examples of some modern lepidopterous pupae showing non-branching pattern such as *Latoia lepida* CRAMER (Fig. 4) etc. In this figure, the tracheae composing a bundle run abreast in parallel to the wing plate, but in some cases they seem to run abreast and perpendicularly to the wing plate. NOHIRA (1947) interpreted the presence of R in a bundle in *Lycaeides argyrognomon oraeterinsularis* VERITY as an abnormal pattern. He also observed many examples of secondary tracheae and extraordinary branching in butterfly pupae. His findings may be explained as follows: that is, the tracheation in ancestral form might have atrophied or have hidden under the bundle in modern Lepidoptera.

It is known that the wing tracheation occurs in the internal wing bud of the last instar larva and that the wing veins are formed at the end of the pupal period, though the embryonic determination of the venation is made at pupation. This is suggested from the fact that the ridges appear on the wing cuticular of the pupa in some species (e.g., *Illiberis rotundata* JORDAN, as shown by the dotted lines in Fig. 8D) or the coarse lines appear on the smooth wing cuticular which is homologous with the adult venation in some species (e.g., *Odites leucostola* MEYRICK). The pupal tracheae penetrate into vein channels. They must be transformed to do so (Fig. 7A) because the arrangement of the tracheae differs markedly from that of the veins. This transformation takes places several days after pupation. NOHIRA (1961) named this period the "undulation stadium." The penetration of trachea into vein channel is not always one to one. For example, in *Epiblema (Notocelia) rosaecolana* DOUBLEDAY (Fig. 8L)  $R_5$  and  $M_1$  penetrate into a vein channel of  $M_1$ . On completion of the vein, the trachea seems to be absorbed into the vein tissue. If the trachea inserted in the vein tissue has activity yet, then it is surely unnatural that the stem vanishes and the branch is active on M of the adult wing. In Cu, it was sometimes observed that  $Cu_2$  vanishing on the adult wing is separated from  $Cu_{1a} + Cu_{1b}$  at the proximal end of Cu stem (Fig. 3). This is significant in relation to the tracheal vanishing. The arborescent tracheoles attendant on the tracheae are often observed in higher Lepidoptera such as the saturniid (Fig. 16A) or the bombycoid (Fig. 15G), in which they are not fully inserted in the vein channel and are recognized distinctly on the adult wing.

### Type of the Pupal Wing Tracheation of Lepidoptera

There are several patterns of the pupal wing tracheation in Lepidoptera. Some of them were listed by MAKIBAYASHI (1979) for butterflies. In the present paper, all of conceivable tracheal patterns are arranged. Before classifying the tracheation patterns, an explanation should be given on the deflective point\* of the tracheae. The deflective points seem to be restricted to the following area on the wing: 1) near

\* In this paper, the word of "branching" or "branching point" is not used from the reason mentioned above. And, also the word of "bundle" was used instead of "stem."

the base, 2) the middle part and 3) the subterminal portion. These points are indicated by symbols according to a modification of the TILLYARD-system in this paper: viz. 1) *f* for the points near the base, *f'* for those in the middle, and *f''* for those in the subterminal, and 2) the initial of each bundle (=stem) name is added before the sign of the deflective point. Consequently, for example, the deflective point of *R*<sub>1</sub> from the bundle of *R* and the point of *Cu*<sub>1a</sub> from the *Cu* bundle are expressed as *rf* and *cuf''*, respectively. In the existing Lepidoptera, *mf*, *mpf''*, and *cuf'* might have been lost as shown in Fig. 2.

The variation of tracheation mainly occurs on three bundles, *R*, *M* and *A*. Fourteen patterns were recognized for *R* (Fig. 5) but three of them could not be examined yet. Though the fundamental pattern in these 14 types is difficult to determine, the pattern *A* in Fig. 5 is presumed to be the fundamental one as it is not only identical with the figure of the insect archetype venation (e.g., SNODGRASS, 1935) but also present universally among various families. Other patterns might have been derived from *A* as shown by the arrows. However, the derivation of the patterns does not occasionally occur in accordance with the arrow marks. This may be due to the crossing of the tracheae. It is difficult to explain reasonably the tangling of radius anterior (*RA*) and radius posterior (*RP*) in the undulation stadium of *Perinaenia accipiter*

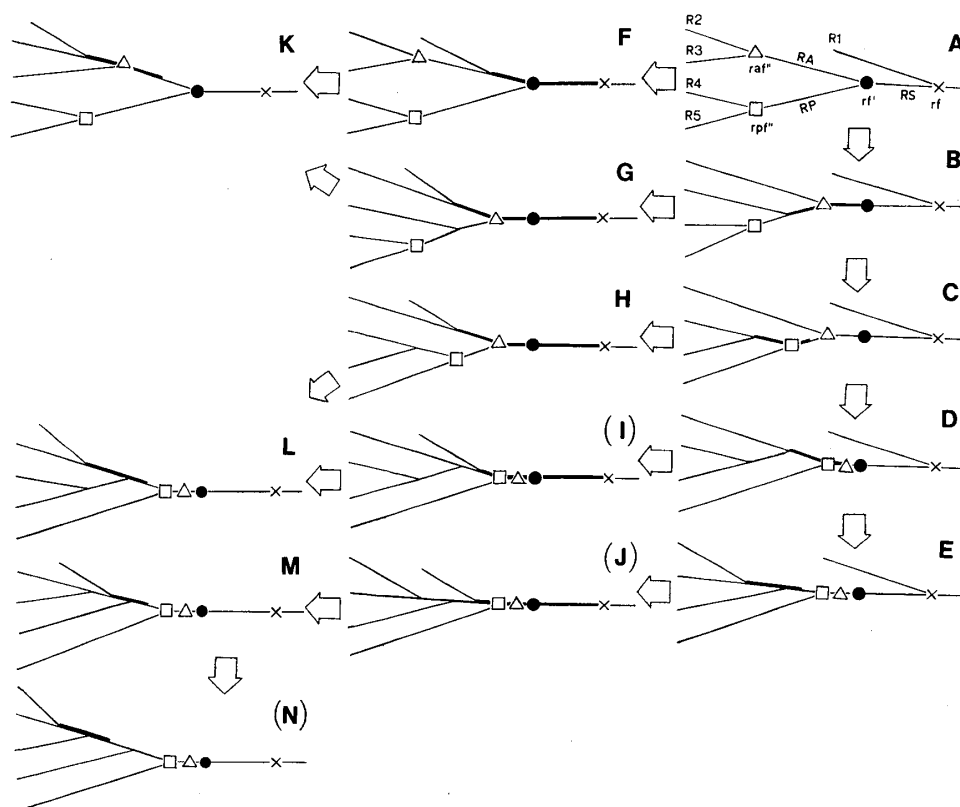
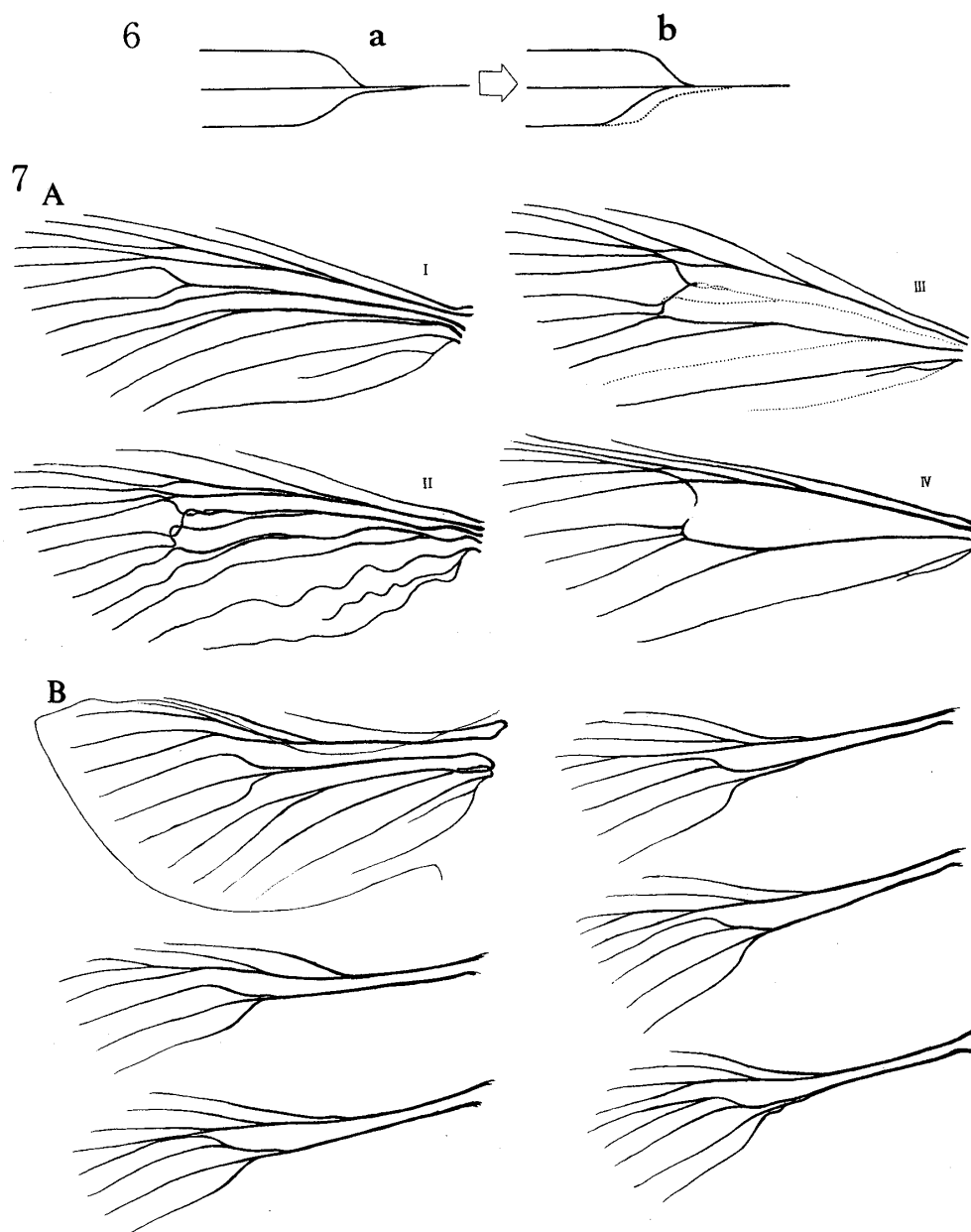


Fig. 5. The tracheal deflexion types in the forewing radius of the lepidopterous pupa and their transformation process. The three types in parentheses could not be examined by the author.  $\times$ ,  $\bullet$ ,  $\triangle$  and  $\square$ : deflective points, *rf*, *rf'*, *raf''* and *rpf''* in the fundamental pattern (*A*-type). Bold line shows the part for the deflective point shifted from an immediate pattern. Other signs refer to the article.

FELDER et ROGENHOFER (Fig. 12A, a). The order of tracheae may be derived independently of the order of tracheal deflexion. In some pyralid species as a result of the crossing of  $R_3$  and  $R_4$  tracheae, type A converts into type C or type F into type H (e.g., Fig. 10F). The same result may also be derived from the contiguity of  $R_3$  and  $R_4$  (Fig. 10E). The contiguity of the basal part of  $R_5$  and radial sector (Rs) in *Anchylo-lomia japonica* ZELLER (Fig. 9P) may conduce to the result of another conversion. If the deflexion of  $R_5$  occurs at the point indicated by the asterisk (\*), the type is D;



Figs. 6-7. Fig. 6. The two tracheal deflexion types of the media. The arrow shows the transforming process between them. Fig. 7. A: The transit of the wing tracheation during the pupal period in *Hylonycta hercules* FELDER et ROGENHOFER (Noctuidae); (I) At just after the pupation; (II, III) at undulation stadium; (IV) adult venation. B: The individual variation in the pupal tracheation of *Arctornis asahinai* INOUE (Lymantriidae).

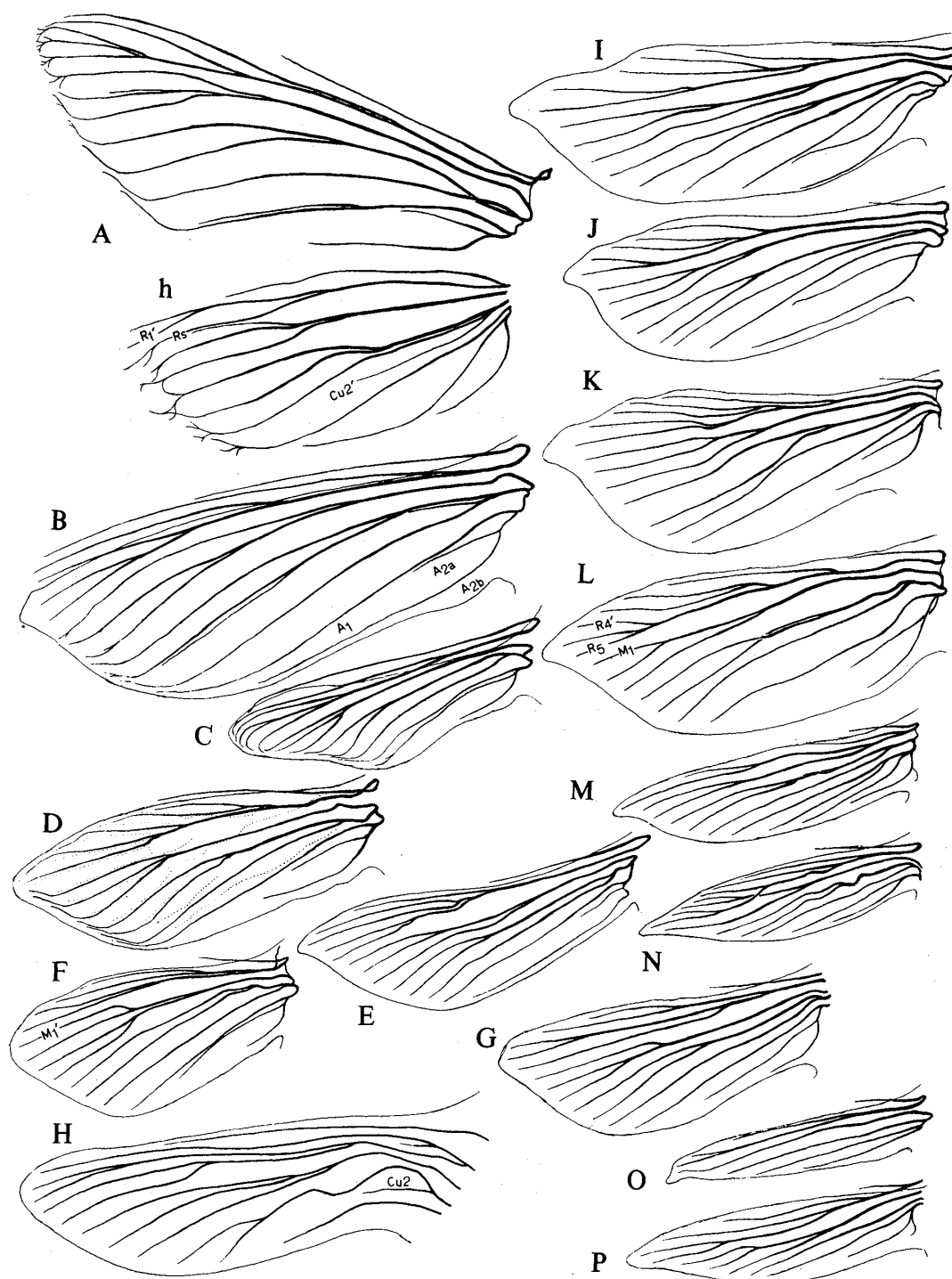


Fig. 8. Pupal wing tracheation. A: *Pidorus glaucopis atratus* BUTLER (Zygaenidae), Sakai, Osaka; (h) hindwing. B: *Chalcosia remota* WALKER (Zygaenidae), Mt. Fuji, Shizuoka. C: *Pryeria sinica* MOORE (Zygaenidae), Mt. Takao, Tokyo. D: *Illiberis rotundata* JORDAN (Zygaenidae), Takaishi, Osaka. E: *Balataea funeralis* BUTLER (Zygaenidae), Takaishi, Osaka. F: *Heterogenea asella* SCHIFFERMÜLLER et DENIS (Limaecodidae), Mt. Shigi-san, Osaka. G: *Eumeta variegata japonica* HEYLAERTS (Psychidae), Takaishi, Osaka. H: *Endoclyta excrescens* BUTLER (Hepialidae), Kawachi-Nagano, Osaka. I: *Archips oporana* LINNAEUS (Tortricidae), Tondabayashi, Osaka. J: *Argyrotaenia angustilineata* WALSINGHAM (Tortricidae), Mt. Fuji, Shizuoka. K: *Dactyloglyphia tonica* MEYRICK (Tortricidae), Shinobu-yama, Osaka. L: *Epiblema (Notocelia) rosaecolana* DOUBLEDAY (Tortricidae), Mt. Kurama,

but if it occurs at the point by double asterisk (\*\*), the type is C. In this case, it can be considered that the latent C-type converted into the actual D-type. In Fig. 5, the A, F and K types are the so-called dichotomous, the B and G pectinate and the C and H semipectinate according to YATA (1981). The D, I and L types are reverse of semipectinate and the E, J, M and N are reverse of pectinate (excepting  $R_1$  in all the cases). The rf is located toward the base from the first deflective point in the A to the E types, between first and second points in the F to the J types, between second and third points in the K to the M types, and toward the tip from the third point in the N type.

The variation of the pattern of M is simpler than that of R. Only two types can be recognized (Fig. 6). The fundamental pattern of M seems to be an a-type (= *Papilio*-type by MAKIBAYASHI, 1978). The conversion of a-type to b-type (= *Luehdorfia*-type by MAKIBAYASHI, 1978) is probably caused by the shift of the deflective point of  $M_3$ , though SNODGRASS (1935) mentioned that the  $M_4$  trachea lost has some bearing. The crossing effect of the tracheae is recognized in M too (Fig. 10 I). Some modified patterns of M were recognized as follows: 1) the pattern in which  $M_1$  and  $M_2$  curve angularly upwards and downwards respectively at deflective points and 2) the pattern in which  $M_1$  and  $M_3$  curve angularly. The former corresponds with the so-called "quadrifid" in the adult venation and the latter with "trifid."

The A vary from one to four in number (three is common). Each of the 2A and 3A is separated from the short common stem which connects with 1A in the type having three A branches as in Cu; that is, 1A, 2A and 3A should be  $A_1$ ,  $A_{2a}$  and  $A_{2b}$  respectively (Fig. 8B). In the type having four A branches, an extra one is secondary but it appears subsidiary to various anal tracheae; e.g. 1A in *Dictyoploca* (Fig. 16A), 2A in *Amphipyra* (Fig. 11H), and 3A in *Botyodes* (Fig. 10B), *Lampides* (Fig. 16F), and in the sphingid species.

### Characteristics of the Pupal Wing Tracheation in Each of the Lepidopterous Families Examined

The pupal wing tracheation of the following 44 families of Lepidoptera were examined.

Hepialidae: R is A-type with a short branch from  $R_1$  presumed to be a vestige of  $R_{1b}$  in *Endoclyta excrescens* BUTLER (Fig. 8H). The rf shifts nearer the base and RA is very long. M is a-type and media anterior (MA) is short.  $Cu_2$  is short and ends far in front of the outer margin. A is 1.

Psychidae: Only *Eumeta variegata* SNELLEN was examined. This species has H-type R, b-type M and 3 in number A.

Limacodidae: Two species were examined. *Latoia lepida* CRAMER has C-type R, b-type M and 3 in number A; 3A is longer than 2A. *Heterogenea asella* SCHIFFERMÜL-

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Kyoto. M: *Agriothera elaeocarpophaga* MORIUTI (Amphitheridae), Yûto near Hamamatsu, Shizuoka. N: *Stathmopoda* sp. (Stathmopodidae), Sakai, Osaka. O: *Phyllonorycter nipponicella* ISSIKI (Gracillariidae), Mt. Takao, Tokyo. P: *Proleucoptera smilactis* KUROKO (Lyonetiidae), Kawachi-Nagano, Osaka.

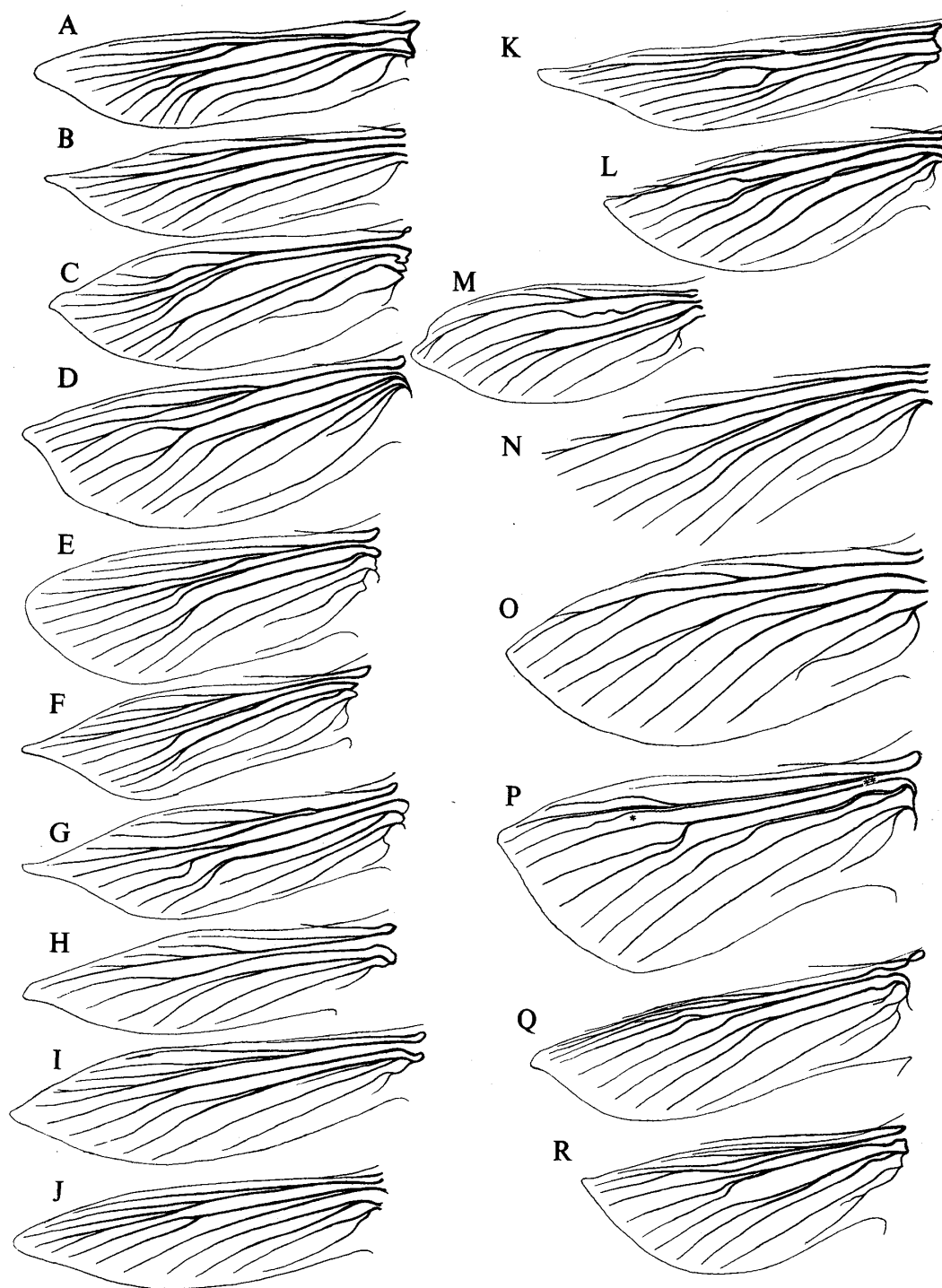


Fig. 9. Pupal wing tracheation. A: *Yponomeuta polystigma* FELDER et FELDER (Yponomeutidae), Kibune, Kyoto. B: *Acrolepiopsis issikiella* MORIUTI (Acrolepiidae), Sakai, Osaka. C: *Hamadaula anisocentra* MEYRICK (Glyphipterygidae), Kawachi-Nagano, Osaka. D: *Odites leucostola* MEYRICK (Lecithoceridae), Sakai, Osaka. E: *Agonopterix issikii* CLARK (Oecophoridae), Mt. Kurama, Kyoto. F: *Dichomeris tostella* STRINGER (Gelechiidae), Kongô, Osaka. G: *Brachmia triannulella* HERRICH-SCHÄFFER (Gelechiidae), Sakai, Osaka. H: *Elachista* sp. (Elachistidae), Mt. Kurama, Kyoto. I: *Pyroderces japonica* KUROKO (Cosmopterigidae), Sakai, Osaka. J: *Scythris sinensis* FELDER et ROGENHOFER (Scythridae), Sakai, Osaka. K: *Oidaematophorus lienigianus* ZELLER (Pterophoridae),



LER et DENIS showed an abnormal pattern; viz. 4 in number R are presumed to have resulted from a loss of  $R_5$  in G-type and 4 in number M are understood to have resulted from appearance of an extra trachea of  $M_1$  to b-type; 3A is shorter than 2A.

Zygaenidae: This family has variable R patterns. Phaudinae have C-type, Chalcosiinae B-type and Zygaeninae A- or G-type. However, transitional patterns of C-type and B-type were seen in *Pidorus* (Chalcosiinae) and *Balataea* (Zygaeninae), respectively. M is b-type in all subfamilies excepting *Balataea funeralis* BUTLER which shows a-type. A is 3 and 3A is longer than 2A excepting Phaudinae.

Tortricidae: Both Tortricinae and Olethreutinae have the same pattern. R is A-type and RA is very short. M is a-type. A is 3 and 2A and 3A are almost of the same length.

Amphitheridae: R is A-type and  $rf'$  shifts to the basal part. M is a-type and A is 2. It is curious that  $cuf'$  shifts to the base.

Phyllocnistiidae: In *Phyllonorycter*, the tracheae are reduced in number as follows: R is 3, M is 1, Cu is 1, and A is 2.

Lyonetiidae: R is reduced to 4 but may be originally A-type. M is a-type and Cu is 1. A is 3.

Gelechiidae: R is A- or F-type (the latter may be abnormal) and RA is short. M is b-type ( $M_3$  is angular or curved near the deflective point). Dichomerini is peculiar in the  $Cu_2$  never reaching to the outer margin. 3A is short or absent.

Oecophoridae: R is A-type and M is a-type. 2A and 3A are nearly the same in length. It is closely allied to the preceding family excepting the differences in the features of M and A tracheae.

Lecithoceridae: The same pattern as in Gelechiidae but RA is very short and  $M_1$  is angular at the deflective point. 2A and 3A are of the same length.

Elachistidae: R is B-type. M is reduced to 2, presumably resulting from a loss of  $M_1$ . A is 2 and 2A is short.

Cosmopterigidae: It is the same pattern as in Elachistidae.

Sathmopodidae: Almost the same pattern as in the above 2 families but M is 3 and a-type. 2A is relatively long.

Scythrididae: Excepting the loss of  $Cu_{1a}$ , the tracheal pattern is the same as that of Sathmopodidae. The  $mf$  shifts to the basal part.

Acrolepiidae: R is A-type and RA is short. M is a-type. A is 2, presumably due to vanishing of 3A.

Yponomeutidae: The pattern is identical with that of Acrolepiidae. According to MORIUTI (1977), Plutellinae, Praydinae and Yponomeutinae have the same pattern.

Glyphipterigidae: Excepting the presence of 3A, this family shows a similar pattern to Yponomeutidae. The  $rf$  migrates near  $rf'$ .

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Kawachi-Nagano, Osaka. L: *Phycitodes unifasciellus* INOUE (Pyralidae), Kauchi-dani, Nara. M: *Calguia* sp. (Pyralidae), Sakai, Osaka. N: *Salebria semirubella* SCOPOLI (Pyralidae), Sakai, Osaka. N: *Salebria semirubella* SCOPOLI (Pyralidae), Takaishi, Osaka. O: *Teliphasa elegans* BUTLER (Pyralidae), Sakai, Osaka. P: *Anchylolomia japonica* ZELLER (Pyralidae), Takaishi, Osaka. Q: *Endotricha theonalis* WALKER (Pyralidae), Takaishi, Osaka. R: *Trichophyestis cretacea* BUTLER (Pyralidae), Takaishi, Osaka.

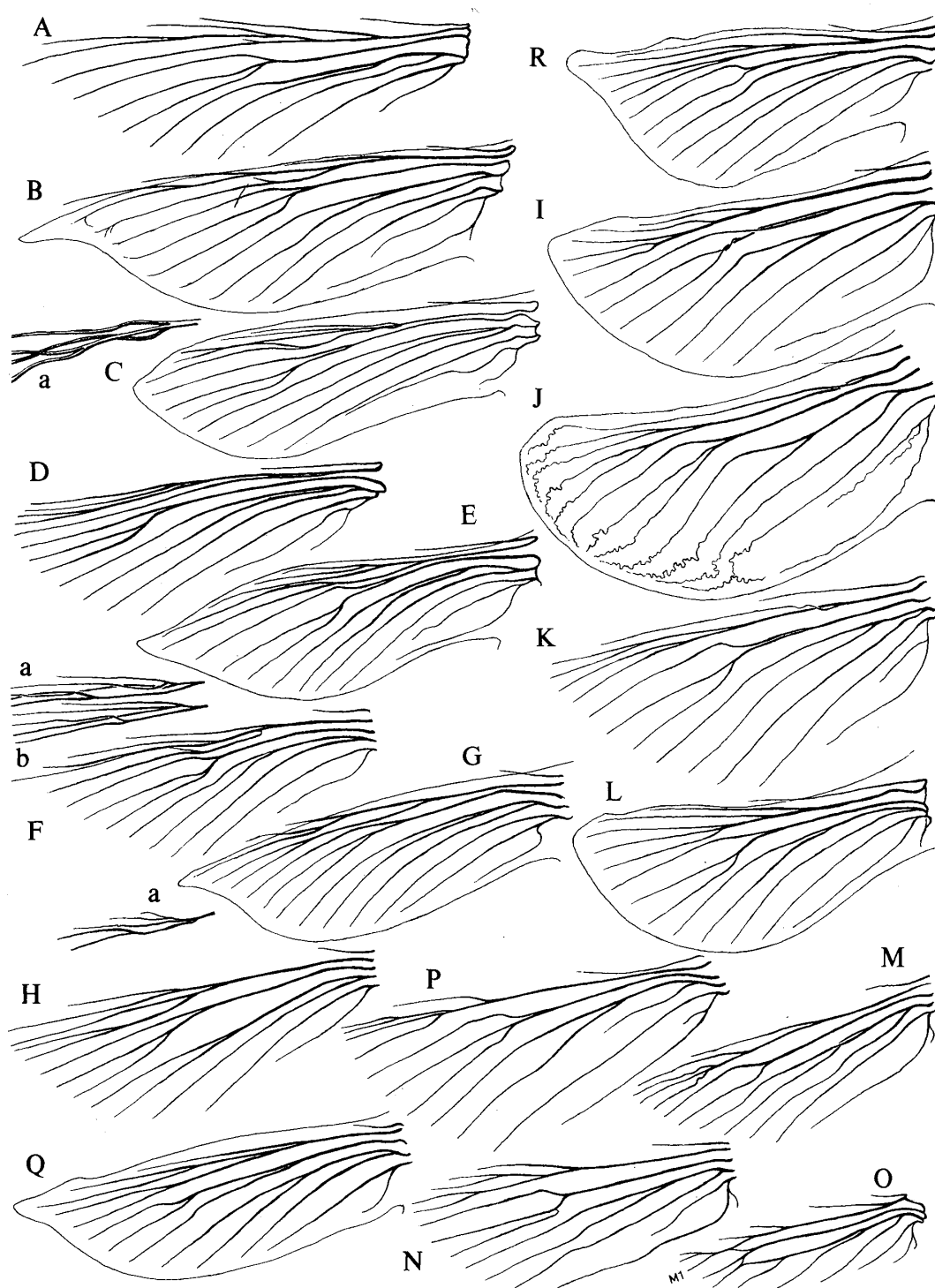


Fig. 10. Pupal wing tracheation. A: *Polythripta liquidalis* LEECH (Pyrilidae), Mt. Takao, Tokyo. B: *Botyodes principalis* LEECH (Pyrilidae), Mt. Kôya, Wakayama. C: *Sinibotys evenoralis* WALKER (Pyrilidae), Mt. Kurama, Kyoto; (a) enlargement of radius (part). D: *Udea testacea* BUTLER (Pyrilidae), Takaishi, Osaka. E: *Nomophila noctuella* DENIS et SCHIFFERMÜLLER (Pyrilidae), Takaishi, Osaka. F: *Palpita nigropunctalis* BUTLER (Pyrilidae), Takaishi, Osaka; (a, b) variants of radius. G: *Chabula onychinalis* GUENÉE (Pyrilidae), Sakai, Osaka; (a) variant of radius. H: *Pleuroptya quadrimaculalis* KOLLAR (Pyrilidae), Mt. Kôya, Wakayama. I: *Hyphantria cunea* DRURY (Arctiidae), Sakai, Osaka. J: *Spilosoma seriato-punctata* MOTSCHULSKY (Arctiidae), Takaishi, Osaka. K: *Spilosoma*

Pterophoridae: In *Oidaematophorus*, R is 4 and it is unknown to the author whether R<sub>1</sub> or R<sub>2</sub> is absent. M is a-type, Cu is 3 and A is 2.

Pyralidae: The pattern varies among the subfamilies. In Phycitinae, R is B-type, M is b-type and A is 3. In Epiphaschiinae and Crambinae, R is C- or D-type, M is b-type and A is 3. In Endotrichinae, R is D-type, M is a-type and A is 3. Ten species of Pyraustinae examined are divided into 5 groups (I–V) as to R pattern. The group I (represented by *Polythlipta liquidalis* LEECH, *Palpita nigropunctalis* BUTLER and *Nomophila noctuella* DENIS et SCHIFFERMÜLLER) is A-type, the group II (*Chabula onychinalis* GUENÉE, *Sinibotys evenoralis* WALKER and *Trichophysestis cretacea* BUTLER) is F-type, the group III (*Agrotera posticalis* WILEMAN) is K-type, the group IV (*Pleuroptya quadrimaculalis* KOLLAR) is G-type and the group V (*Udea testacea* BUTLER) is L-type. *Botyodes principalis* LEECH has variants which are regarded A-, F- or K-type. The species of the group I seemingly show the C-type because of the crossing effect. In all the groups, M is b-type and A is 2 or 3.

Thyrididae: R is A-type, M is a-type and A is 2.

Nolidae: The tracheal pattern involves C-type R and a-type M. A is 3 and 3A is the shortest.

Noctuidae: More than 40 species comprising all the Japanese subfamilies were examined and the same tracheal pattern was recognized in almost all the examined species. R is A-type, M is a-type and A is 3. 2A is the shortest in general but 3A is the shortest in some species. RA and RP are of the same length in many species but the shorter RA is recognized in a few species. M<sub>1</sub> and M<sub>2</sub> are angular or curved at the deflective point and M<sub>3</sub> runs sinuate along M<sub>2</sub> in general. *Microxylla confusa* WILEMAN shows D-type R and b-type M and "*Rivula*" *curvifera* WALKER shows B-type R and b-type M.

Agaristidae: The pattern is the same as that of Noctuidae.

Sarothripidae: Two types of tracheal patterns are recognized. *Pseudoips fagana* FABRICIUS has a-type M and the shortest 2A which is the same as that of Noctuidae, and other species examined have b-type M and the shortest 3A. R is A-type.

Arctiidae: Two types, A and B, of R are recognized in Arctiinae and Lithosiinae. M is b-type and A is 3 but 2A is the shortest in Arctiinae and 3A is the shortest in Lithosiinae.

Ctenuchidae: R is A-type and RP is very short. M is b-type and A is the same as that of Arctiinae.

Lymantriidae: Two tracheal patterns are recognized. Lymantriini shows a pattern having C-type R and a-type M (*Arctornis asahinai* INOUE which has A- or C-type R and b-type M is exceptional species in this tribe, see Fig. 7B); on the other hand, Orgyiini have A- or B-type R and b-type M. *Euproctis* (Lymantriini) shows conversely the

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*flammeola* MOORE (Arctiidae), Sakai, Osaka. L: *Stigmatophora flava* BREMER et GREY (Arctiidae), Kawachi-Nagano, Osaka. M: *Conilepia nigricosta* LEECH (Arctiidae), Sagami-ko, Kanagawa. N: *Lithosia quadra* LINNAEUS (Arctiidae), Amami, Osaka. O: *Chamaita ranruna* MATSUMURA (Arctiidae), Amami, Osaka. P: *Amata fortunei* ORZA (Ctenuchidae), Sakai, Osaka. Q: *Rhodoneura pallida* BUTLER (Thyrididae), Shinobu-yama, Osaka. R: *Striglina cancellata* CHRISTOPH (Thyrididae), Shinobu-yama, Osaka.

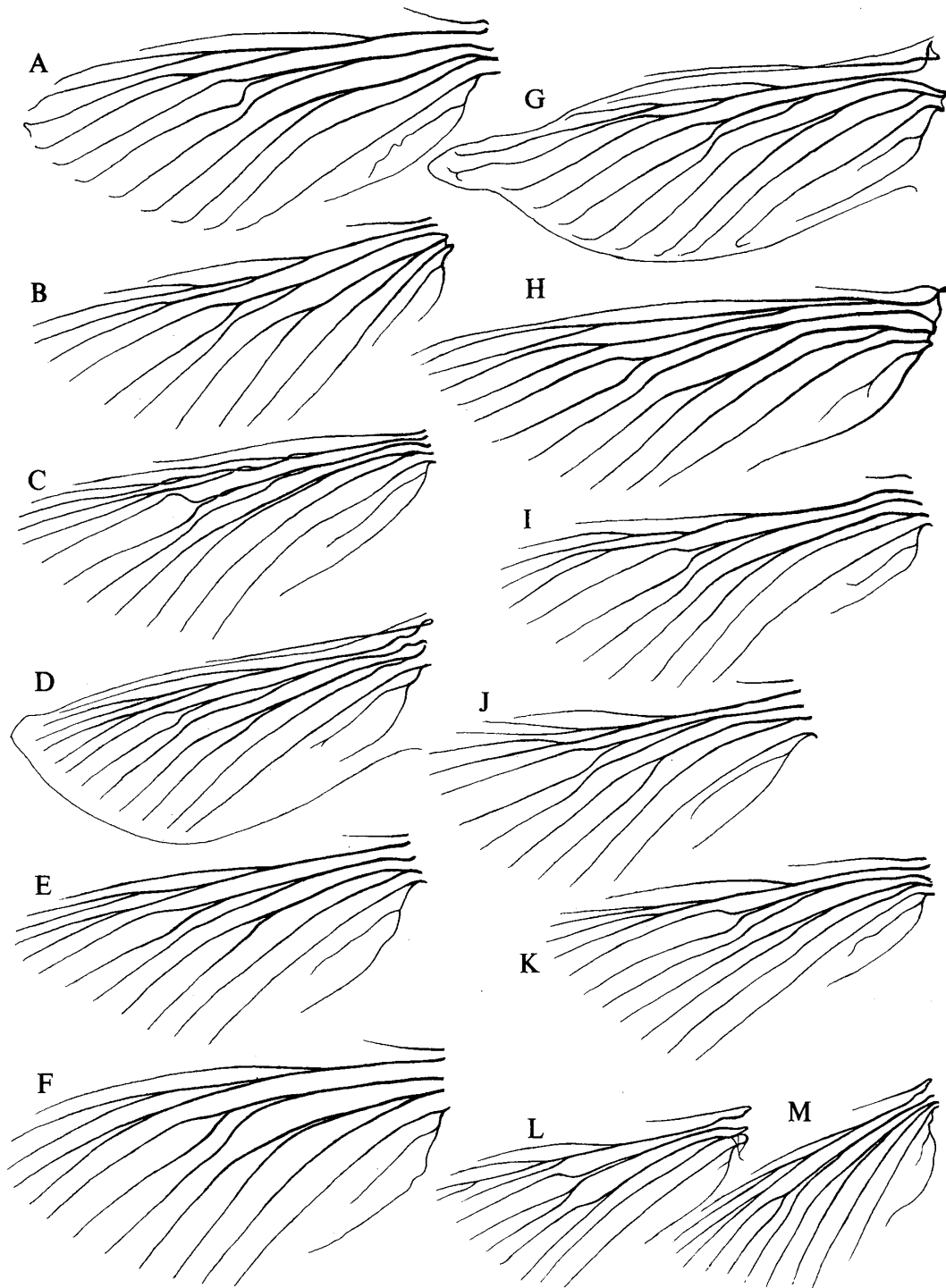


Fig. 11. Pupal wing tracheation. A: *Hylonycta hercules* FELDER et ROGENHOFER (Noctuidae), Sakai, Osaka. B: *Helicoverpa armigera* HÜBNER (Noctuidae), Takaishi, Osaka. C: *Diarsia pacifica* BOURSIN (Noctuidae), Sakai, Osaka. D: *Peridroma saucia* HÜBNER (Noctuidae), Sakai, Osaka. E: *Mamestra brassicae* LINNAEUS (Noctuidae), Sakai, Osaka. F: *Brithys crini* FABRICIUS (Noctuidae), Daiôzaki, Mie. G: *Ctenoplusia albostrata* BREMER et GREY (Noctuidae), Sakai, Osaka. H: *Amphipyra erebina* BUTLER (Noctuidae), Mt. Shiroyama, Tokyo. I: *Spodoptera litura* FABRICIUS (Noctuidae), Sakai, Osaka. J: *Hadjina biguttula* MOTSCHULSKY (Noctuidae), Takaishi, Osaka. K: *Nipponyx segregata* BUTLER (Noctuidae), Sakai, Osaka. L: *Microxyla confusa* WILEMAN (Noctuidae), Ozenji, Kawasaki. M: *Callopietria japonibia* INOUE et SUGI (Noctuidae), Amami, Osaka.

same pattern as Orgyiini excepting the short 3A. The close relationship between *Euproctis* and the genera of Orgyiini is also recognized in the morphology of the pupa (NAKAMURA, 1976).

Thyatiridae: R is A-type and M is a-type. A is 2.

Drepanidae: R is A-type but in *Psiloreta* F-type and M is b-type. A is 2.

Notodontidae: The pattern of R varies from genus to genus. M is a-type and A is 2 or 3 in all the species examined. R is A-type in *Cerura*, *Furcula*, *Torigea* and *Phalera*, C-type in *Stauropus*, *Notodonta*, *Peridea*, *Drymonia*, *Hexafrenum*, *Ptilophora* and *Pterostoma*, D-type in *Phalerodonta* and *Clostera* and H-type in *Neostauropus*. R of *Micromelalopha* is reduced to 4 and seems to be D-type originally.

Geometridae: The pattern varies among the subfamilies. In Sterrhinae, R is C-type, M is a-type and A is 2 but the R of *Organopoda* shows A-type. Geometrinae is the same in the tracheation as Sterrhinae but A is 3. The tracheation of Larentinae is variable. R is A- or B-type and occasionally changes to F-type (*Episteira* and *Hetero-thera*) or G-type (*Nothoporia*). M is a-type excepting *Eupithecia* of b-type. A is 3. R of Ennominae shows 2 types; in the most species it is C-type but in *Calospilos*, *Philobia*, *Auaxa*, *Zanclidia*, *Ourapteryx*, and etc. it is A-type. M is a-type but is b-type in *Calospilos*. A is 3. *Alsophila* has C-type R and a-type M, while *Inurois* has A-type R and b-type M.

Sphingidae: R is originally A-type but the atrophy of  $R_2$  becomes more pronounced in order of Smerinthini, Sphingini, Dilophonotini and Macroglossini. In Macroglossini, R becomes 4 finally. M is a-type and A is 4 or 5 which is accompanied by short tracheae to  $A_2$  and/or  $A_3$ . The spaces between  $Cu_{2a}$  and  $Cu_{2b}$  and between  $Cu_{2b}$  and  $A_1$  are narrower than those between other tracheae.

Brahmaeidae: R is M-type and M is a-type. Short  $Cu_{1a'}$  is present. A is 3.

Eupterotidae: R is 4 which may be due to the loss of  $R_3$ . M is a-type. A is 3 and  $A_2$  is the shortest among them.

Lasiocampidae: R is A-type (in *Malacosoma*) or F-type (in *Philudoria*). M is b-type. Cu is 4, with  $Cu_{1a'}$  lying contiguous with  $M_3$ . A is 2 or 3.

Bombycidae: The tracheation of *Bombyx mandarina* MOORE was examined. R is B-type, M is a-type and A is 3.

Saturniidae: Concerning R, *Actias* is E-type with reduced  $R_5$ , *Dictyoploca* K-type with reduced  $R_3$  and  $R_5$ , and *Antheraea* is 3, which is presumably A-type without  $R_3$  and  $R_5$ . M is a-type and A is 3. However, in *Dictyoploca*, M is 2, with  $M_1$  lost and  $M_3$  atrophied. Cu is 4 and A is 3.

Hesperiidae: R is F-type and M is a-type (MAKIBAYASHI and HIROHATA (1980) illustrated an abnormal pattern of M in *Potanthus flavum* MURRAY, see Fig. 16M for accurate pattern). Both Cu and A are 3.

Papilionidae: R is F-type and *Parnassius* is lacking in  $R_3$  (MAKIBAYASHI & HIROHATA, 1980), M is a-type, Cu is 3 and A is 2. Only *Luehdorfia* has K-type R and b-type M (NOHIRA, 1948).

Pieridae: The tracheation is the most varied among the Japanese butterfly families. After YATA (1981), R lacks  $R_5$  in general but has an extra trachea in most species. *Leptidea* has 5 tracheae and *Anthocharis* further adds one extra trachea.

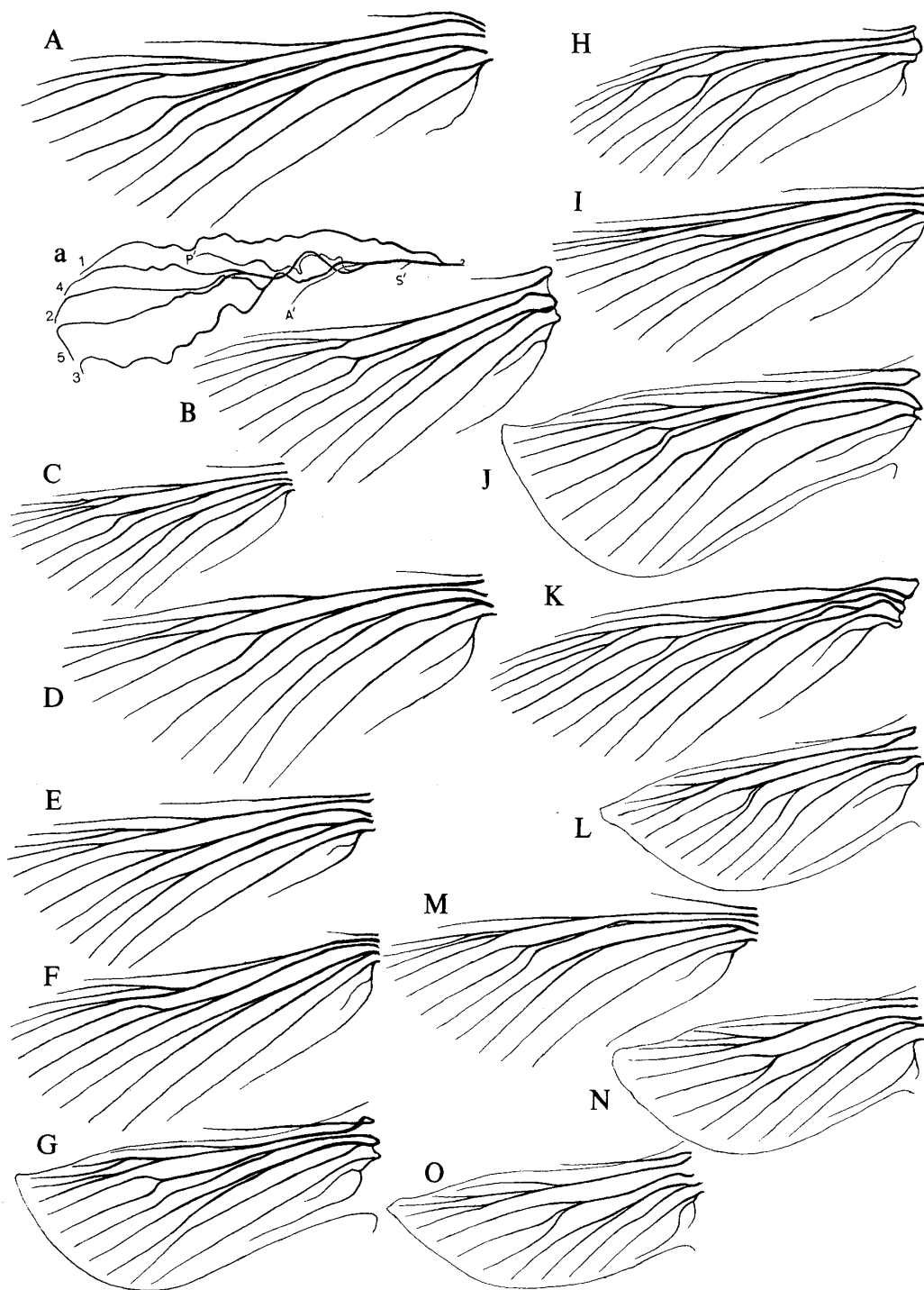


Fig. 12. Pupal wing tracheation. A: *Perinaenia accipiter* FELDER et ROGENHOFFER (Noctuidae), Zushi, Kanagawa; (a) radius at undulation stadium (A', extra trachea of RA; P', extra trachea of RP; S', extra trachea of Rs; 1 to 5, R<sub>1</sub> to R<sub>5</sub>). B: *Xanthodes transversa* GUENÉE (Noctuidae), Sakai, Osaka. C: *Micardia argentata* BULTER (Noctuidae), Ozenij, Kawasaki. D: *Dinumma deponens* WALKER (Noctuidae), Kawachi-Nagano, Osaka. E: *Colobochyla salicalis* DENIS et SCHIFFERMÜLLER (Noctuidae), Sakai, Osaka. F: *Plusiodonta coelonota* KOLLAR (Noctuidae), Daiôzaki, Mie. G: *Pangrapta obscurata* BULTER (Noctuidae), Sakai, Osaka. H: *Zanclognatha lilacina* BUTLER (Noctuidae), Kawachi-Nagano, Osaka. I: *Eutelia adulatricoides* MELL (Noctuidae), Takaishi, Osaka. J: *Sarbanissa subflava*

These original patterns of R are presumed to be F-type, B-type (*Appias*) or C-type (*Artogeia*). M is a-type but frequently lacks M<sub>1</sub>. Both Cu and A are 3.

Lycaenidae: The number of R reduces to 4 and may originally be A- or F-type but 1 extra trachea appears in the species of Lycaeninae (*Lycaeides argyrognomon praeterinsularis* VERITY (NOHIRA, 1948), *Celastrina puspa umenonis* MATSUMURA (MAKIBAYASHI, 1979), *Zizeeria maha argia* MÉNÉTRIÈS, *Lampides boeticus* LINNAEUS). M is a-type. According to MAKIBAYASHI (1979), *Neozephyrus taxila japonicus* MURRAY has b-type but this observation probably be a mistake. Both Cu and A are 3.

Curetidae: R is 4 and probably be led from F-type. M is a-type, Cu is 3 and A is unillustrated (according to MAKIBAYASHI, 1979).

Nymphalidae: R is F-type (the observations of *Apatura* by MAKIBAYASHI (1979) and of *Hestina* by MAKIBAYASHI and HIROHATA (1980) are incorrect). M is a-type, Cu is 3 and A is 2.

Satyridae: R shows B- or F-type. M is a-type, Cu is 3 and A is 2.

Danaidae: Only 1 species, *Caduga sita nipponica* MOORE has been reported by NOHIRA (1949). R is F-type but 1 extra trachea appears in some individuals. M is a-type, Cu is 3 and A is 2.

### Tendency of the Variation of the Pupal Wing Tracheation of Lepidoptera

According to Table 1 and Fig. 5, the followings may be concluded. (1) in many families, the pattern of pupal wing tracheation does not vary within a family; (2) the pleural patterns appearing in a given family are the adjoining patterns in Fig. 5; (3) the following families have several patterns: Zygaenidae of Section\* II, Pyralidae of Section IV, Geometridae and Notodontidae of Section V, and Pieridae and Saturniidae of Section VI; (4) the patterns other than A-E types usually appear in the families of Section VI. Concerning M, the a-type was seen in most of the families examined, and in a few families both a- and b-types were observed. Cu and A irregularly vary.

The number of R varies from 2 to 6. In general, the number of R increases near M and decreases in order of R<sub>3</sub>, R<sub>5</sub> and R<sub>1</sub>. The number of M varies from 1 to 5. The tendency of increase or decrease was recognizable in also M. The increase of trachea appears to give the same pattern to both subbundles, MA and MP (media posterior), and in other word, the increase of trachea appears near R in b-type. While, the decrease of trachea occurs by the disappearance of the outer tracheae beyond mf". There are 3 and 4 tracheae in Cu, namely 1 trachea adds to the fundamental pattern. In this case, the extra trachea shows the M side of the bundle.

\* Section is a category higher than superfamily being proposed tentatively based on the pupal morphology, see NAKAMURA (1981).

MOORE (Agaristidae), Shinobuyama, Osaka. K: *Macrochthonia fervens* BUTLER (Sarrothripidae), Takihata, Osaka. L: *Nycteola asiatica* KRULIKOWSKI (Sarrothripidae), Shinobuyama, Osaka. M: *Pseudoips fagana* FABRICIUS (Sarrothripidae), Mt. Takao, Tokyo. N: *Gabala argentata* BUTLER (Sarrothripidae), Takihata, Osaka. O: *Negritothripa hampsoni* WILEMAN (Sarrothripidae), Kawachi-Nagano, Osaka.

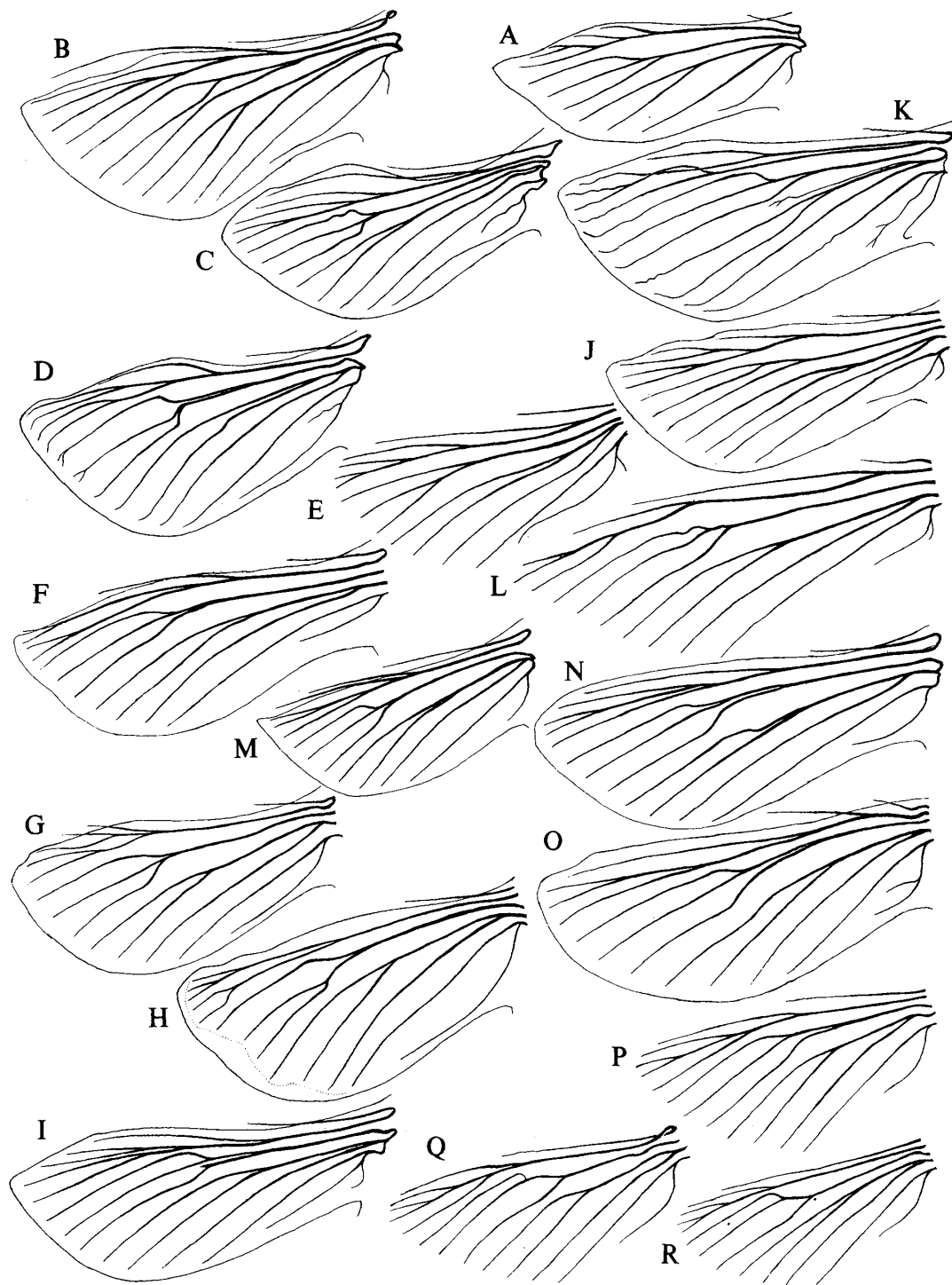


Fig. 13. Pupal wing tracheation. A: *Mimerastris mandschriana* OBERTHÜR (Nolidae), Kishiwada, Osaka. B: *Lymantria dispar* LINNAEUS (Lymantriidae), Sakai, Osaka. C: *Orgyia thyellina* BUTLER (Lymantriidae), Takaishi, Osaka. D: *Cifuna eurydice* BUTLER (Lymantriidae), Takihata, Osaka. E: *Euproctis piperita* OBERTHÜR (Lymantriidae), Takaishi, Osaka. F: *Neoploca arctipennis* BUTLER (Thyatiridae), Mt. Kurama, Kyoto. G: *Callidrepana palleola* MOTSCHULSKY (Drepanidae), Amami, Osaka. H: *Psiloreta pulchripes* BUTLER (Drepanidae), Ozenji, Kawasaki. I: *Phalera takasagoensis* MATSUMURA (Notodontidae), Kawachi-Nagano, Osaka. J: *Furcula lanigera* BUTLER (Notodontidae), Takihata, Osaka.



In many cases, disappearance of a given trachea in one of the bundles results in appearance of an extra trachea in the neighbouring bundle and the whole tracheae of the wing remain the same in number. For example, if M decreases to 2, then R increases to 6 or Cu to 4. However, there are cases where R increase as in *Epiblema* (*Notocelia*) *rosaecolana* DOUBLEDAY (Fig. 8L) or M increase as in *Heterogenea asella* SCHIFFERMÜLLER et DENIS (Fig. 8F), in spite of the tracheae of other bundles showing the fundamental pattern. These examples are often found in generalized families but have also been reported on butterflies, e.g. 4 Cu in Nymphalidae by COMSTOCK (1918) and MAKIBAYASHI (1979); it may be a phenomenon which occurs in all lepidopterous families. In such a case, so extreme contiguity occurs between 2 neighbouring tracheae after the undulation stadium that 1 trachea seemingly vanishes on the wing and the tracheal number becomes the same as in the adult venation.

On the other hand, it is observed that the decrease of trachea happens without appearance of an extra trachea in the neighbouring bundle in some species. This is commonly found on the pupae of leaf-mining species of Sections III and IV but also on the pupae of higher lepidopterous species of Section VI such as Pieridae, Lycaenidae, Sphingidae and Saturniidae. The number of the adult veins also decreases in this case. The bundles in the pupal tracheation of the butterflies of Papilionoidea become curved or angular.

Concerning the pupal tracheation of the hindwing, COMSTOCK (1918) pointed out that the humeral trachea is secondary, differing from Sc for the following reasons: (1) it is absent in the forewing; (2) the generalized family such as Cossidae never possesses it; (3) many humeral tracheae appear only in some families (e.g. Lasiocampidae). However, even if it is secondary, this trachea is distinctly a member of Sc bundle. It seems to be significant that the humeral trachea occurs in the moths such as the sphingid (Fig. 15A); it is never recognized in the adult venation.

The disappearance of R in the hindwing is well known. It has been treated that R comprises  $R_1$  and  $R_s$  (Fig. 15A, h). R of *Graphium sarpedon nipponum* FRUHSTORFER is also 2 but it may be explained more plausibly as  $R_1 + RA$  and RP. Moreover, 3 R are recognized in *Pidorus glaucopis atratus* BUTLER (Fig. 8A, h) and indicated as  $R_1$ , an extra trachea of  $R_1$  and  $R_s$  in this paper but these tracheae may be  $R_1$ , RA and RP or  $R_1$ ,  $R_2$  and  $R_3 + R_4 + R_5$ . This pattern is identical with the most atrophied pattern of R in the forewing, which does not eliminate the possibility of the hindwing tracheae comprising  $R_2$  and  $R_4$  but not  $R_1$  and  $R_s$ . The two types of M are mentioned above and it must be noted that the type often differs between fore and hindwings in a given individual (Figs. 8A, 15A). However, all the butterflies which have been examined showed the same type of M in both wings.

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K: *Neostauropus basalis* MOORE (Notodontidae), Kawachi-Nagano, Osaka. L: *Stauropus fagi* LINNAEUS (Notodontidae), Shinobuyama, Osaka. M: *Ptilophora nohirai* MATSUMURA (Notodontidae), Kibune, Kyoto. N: *Phalerodonta manleyi* LEECH (Notodontidae), Takaishi, Osaka. O: *Pterostoma sinica* MOORE (Notodontidae), Kawachi-Nagano, Osaka. P: *Clostera curtuloides* ERSCHOFF (Notodontidae), Yunomaru Pass, Gumma. Q: *Clostera anastomosis* LINNAEUS (Notodontidae), Sakai, Osaka. R: *Micromelalopha troglodyta* GRAESER (Notodontidae), Kawachi-Nagano, Osaka.

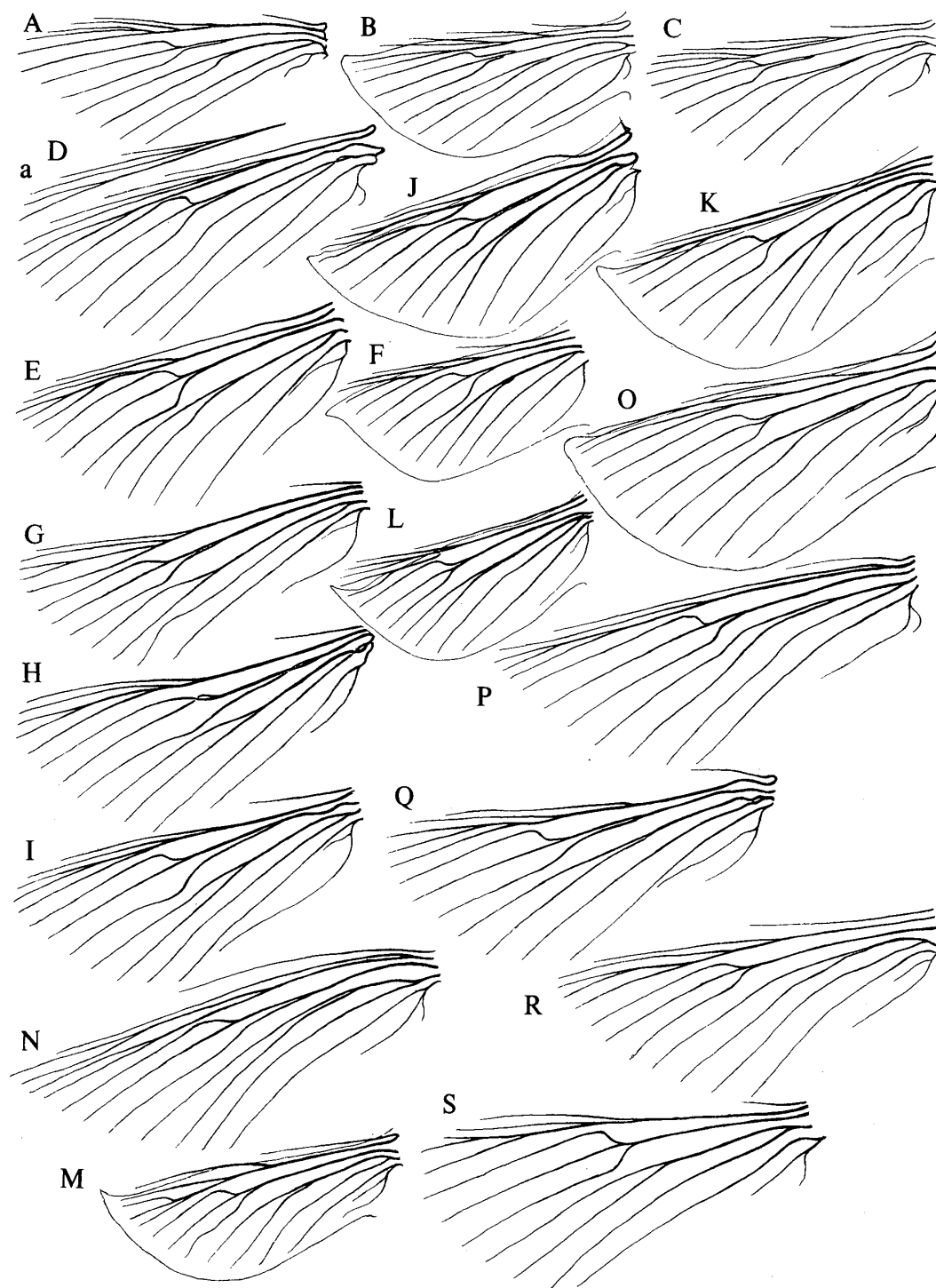


Fig. 14. Pupal wing tracheation. A: *Scopula confusa* BUTLER (Geometridae), Shinobuyama, Osaka. B: *Eupithecia proterva* BUTLER (Geometridae), Sakai, Osaka. C: *Nothoporia mediolineata* PROUT (Geometridae), Mt. Kurama, Kyoto. D: *Heterothera postalbida* WILEMAN (Geometridae), Tondabayashi, Osaka; (a) variant of radius. E: *Agathia curvifiniens* PROUT (Geometridae), Ozenji, Kawasaki. F: *Comibaena procumbaria* PRYER (Geometridae), Yûtô near Hamamatsu, Shizuoka. G: *Thalassodes subquadraria* INOUE (Geometridae), Sakai, Osaka. H: *Hemithea marina* BUTLER (Geometridae), Mt. Takao, Tokyo. I: *Diplodesma ussuriaria* BREMER (Geometridae), Kisarazu, Chiba. J: *Ecliptopera*

Table 1. The variation of the radius in pupal wing tracheation in the lepidopterous families studied.

Section	Family	Type	A B C D E					F G H I J					K L M N			
			A	B	C	D	E	F	G	H	I	J	K	L	M	N
II	Hepialidae		×													
	Psychidae									×						
	Limacodidae				×				×							
	Zygaenidae		×	×	×				×							
III	Amphitheridae		×													
	Tortricidae		×													
IV	Lecithoceridae		×													
	Oecophoridae		×													
	Gelechiidae		×					×								
	Elachistidae			×												
	Cosmopterigidae			×												
	Stathmopodidae			×												
	Scythrididae			×												
	Acrolepiidae		×													
	Yponomeutidae		×													
	Glyphipterigidae		×													
	Thyrididae		×													
	Pyalidae		×	×	×	×		×	×				×	×		
V	Nolidae				×											
	Noctuidae		×	×		×										
	Agaristidae		×													
	Sarothripidae		×													
	Ctenuchidae		×													
	Arctiidae		×	×												
	Lymantriidae		×	×	×											
	Thyatiridae		×													
	Drepanidae		×					×								
	Geometridae		×	×	×			×	×							
	Notodontidae		×		×	×				×						
VI	Sphingidae		×													
	Brahmaeidae													×		
	Lasiocampidae		×					×								
	Bombycidae			×												
	Saturniidae		×				×						×			
	Hesperiidae							×								
	Papilionidae							×					×			
	Pieridae			×	×			×								
	Lycaenidae		×					×								
	Curetidae							×								
	Nymphalidae							×								
	Satyridae			×				×								
	Danaidae							×								

*decurrens illitata* WILEMAN (Geometridae), Ozenji, Kawasaki. K: *Larerrannis miracula* PROUT (Geometridae), Kashimada, Kawasaki. L: *Inurois tenuis* BUTLER (Geometridae), Mizonokuchi, Kawasaki. M: *Alsophila japonensis* WARREN (Geometridae), Kashimada, Kawasaki. N: *Ourapteryx nivea* BUTLER (Geometridae), Mt. Kurama, Kyoto. O: *Abraxas miranda* BUTLER (Geometridae), Sakai, Osaka. P: *Synegia esther* BUTLER (Geometridae), Ozenji, Kawasaki. Q: *Alcis grisea* BUTLER (Geometridae), Tondabayashi, Osaka. R: *Trigonoptila latimarginaria* LEECH (Geometridae), Sakai, Osaka. S: *Cystidia truncangulata* WEHRLI (Geometridae), Ozenji, Kawasaki.

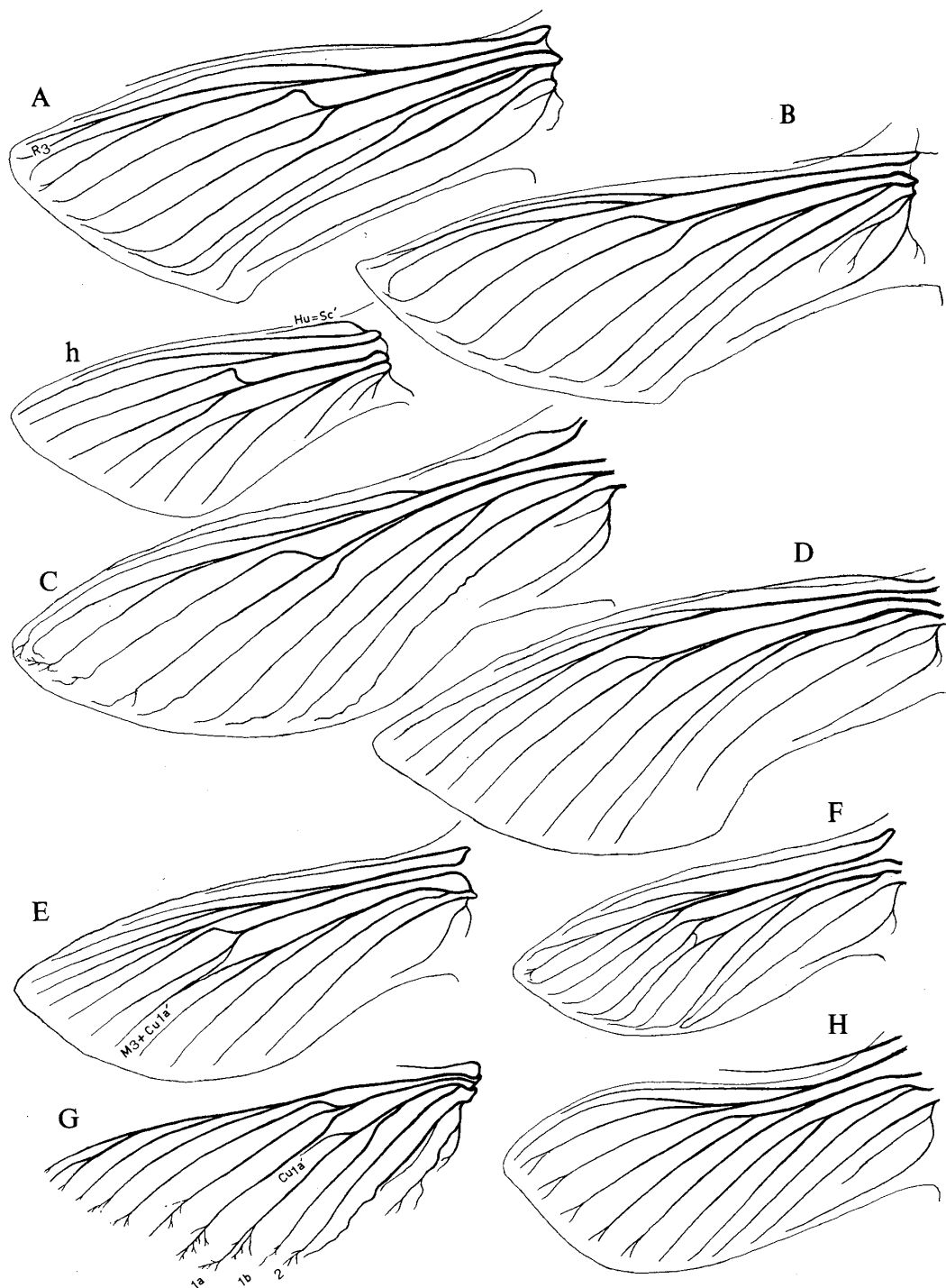


Fig. 15. Pupal wing tracheation. A: *Marumba sperchius* MÉNÉTRIÈS (Sphingidae), Kawachi-Nagano, Osaka; (h) hindwing (Hu: humeral vein). B: *Psilogramma increta* WALKER (Sphingidae), Takaishi, Osaka. C: *Cephonodes hyalis* LINNAEUS (Sphingidae), Sakai, Osaka. D: *Theretra oldenlandiae* FABRICIUS (Sphingidae), Sakai, Osaka. E: *Philudoria albomaculata* BREMER (Lasiocampidae), Mt. Kurama, Kyoto. F: *Malacosoma neustria* LINNAEUS (Lasiocampidae), Takaishi, Osaka. G: *Brahmaea wallichii* GREY (Brahmaeidae), Zushi, Kanagawa. H: *Apha aequalis* FELDER (Eupterotidae), Yûtô near Hamamatsu, Shizuoka.

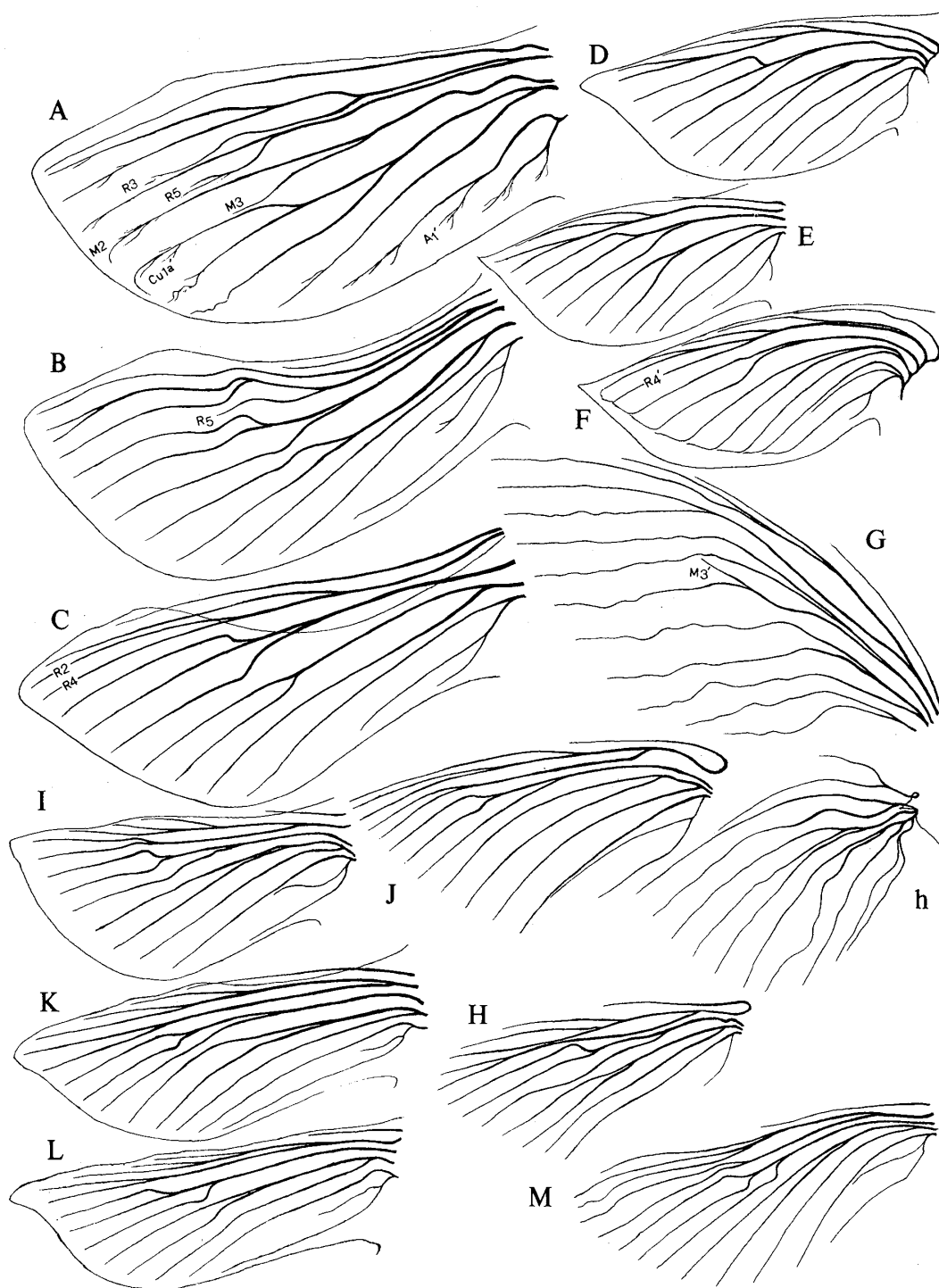


Fig. 16. Pupal wing tracheation. A: *Dictyoploca japonica* MOORE (Saturniidae), Shinobuyama, Osaka. B: *Actias gnoma* BUTLER (Saturniidae), Owakudani, Hakone, Kanagawa. C: *Antheraea yamamai* GUÉRIN-MÉNEVILLE (Saturniidae), Shinobuyama, Osaka. D: *Lycaena phlaeas daimio* SEITZ (Lycaenidae), Takaishi, Osaka. E: *Favonius orientalis* MURRAY (Lycaenidae), Mizonokuchi, Kawasaki. F: *Lampides boeticus* LINNAEUS (Lycaenidae), Takaishi, Osaka. G: *Graphium sarpedon nipponum* FRUHSTORFER (Papilionidae), Sakai, Osaka; (h) hindwing. H: *Neptis aceris intermedia* W. B. PRYER (Nymphalidae), Ozenji, Kawasaki. I: *Daimio tethys* MÉNÉTRIÈS (Hesperiidae), Ozenji, Kawasaki. J: *Choaspes benjamini japonica* MURRAY (Hesperiidae), Ozenji, Kawasaki. K: *Potanthus flavum* MURRAY (Hesperiidae), Amami, Osaka. L: *Thoressa varia* MURRAY (Hesperiidae), Amami, Osaka. M: *Polygonia c-aureum* LINNAEUS (Nymphalidae), Komoro, Nagano.

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## 摘 要

## 鱗翅類の蛹前翅気管系 (中村正直)

現生鱗翅類の蛹前翅気管系は、5本の幹気管から分枝する15本前後の気管から成るとされている。このうち径脈と中脈とは、種によって分枝の形式が殊に著しく変化する。日本産鱗翅類44科についてこの変化を調べ、径脈では理論的に14の形式がありうることを、日本産の種では、そのうち11の形式が認められたこと、中脈には2形式があり、3本の中脈の分枝点における彎曲の仕方でも成虫翅脈における trifid と quadrifid の違いが生ずること等が明らかにされた。3本の臀脈は1本の幹気管から派生するのではなく、まず 1A と 2A+3A とが分れ、その後 2A と 3A とが分れるので、これらは正しくは  $A_1$ ,  $A_{2a}$ ,  $A_{2b}$  と呼ぶべきであろう。

ヒロヘリアオイラガ *Latoia lepida* CRAMER 等の蛹前翅気管系の観察からみて、これらの気管は幹気管から分枝するものではなく、元来はすべて肩部から発し、5組の束になって走り、途中から1本ずつ遊離するものであったと推定される。

蛹翅の気管系の形式は、既に幼虫の翅芽形成期に決定されていることが知られている。成虫翅脈の形式も少くとも蛹化時には決定されていると考えられるので、蛹翅の気管系は蛹期末に翅脈が形成される際に、次第に変化していくものではなく、既定の筋書に沿って翅脈中に嵌合していくものとみなすべきであろう。中脈で気管の基部が消失し、末端のみ活きているとみるのは、いかにも不自然であるので、気管は翅脈が形成される過程で翅脈管中に挿入され、それと共に役割が振替わるものと考えられる。前記の中脈における2つの形式は、蝶を除き多くの場合、同一個体の前、後翅において異っていることは興味あることである。